

LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF *DIOXYNA PICCIOLA* (BIGOT) (DIPTERA: TEPHRITIDAE) ON *COREOPSIS* SPP. (ASTERACEAE) IN SOUTHERN CALIFORNIA

DAVID H. HEADRICK, RICHARD D. GOEDEN, AND JEFFREY A. TEERINK

Department of Entomology, University of California, Riverside, CA 92521, U.S.A.

Abstract.—*Dioxyna picciola* (Bigot) is bivoltine or trivoltine and oligophagous primarily on *Coreopsis* and *Bidens* spp. in southern California. It is a late-stage, aggregated attacker in flower heads at or past anthesis. Mating and oviposition by overwintered F₂ and F₃ adults occurs in spring on wild and cultivated *Coreopsis* spp. Eggs are inserted into soft achenes in which the first two instars and most early-third instars feed solitarily; the late-third instars also feed on sap, and at higher larval densities, score the receptacles and feed on sap accumulated in shallow depressions. Pupariation occurs in heads, with puparia resting in the feeding depressions, or in flower heads containing only a single larva, within hollowed out achenes and situated well above the receptacle. Adults are synovigenic, sexually immature at eclosion, but exceptionally long-lived as the overwintering stage. This tephritid is known in North America as *D. picciola*, but it recently was synonymized with the cosmopolitan *D. sororcula*, but unlike the latter species, Nearctic flies have not been reported from *Calendula officinalis* L. The egg is described and illustrated and differs from the eggs of two other species in the closely related genus *Campiglossa* (= *Paroxyna*) by the elongate, apically expanded pedicel, which bears aeropyles apically. First through third instars and the puparium also are described and illustrated. Third instars of *D. picciola* are similar in morphology to those of *Campiglossa genalis* (Thomson), but are more elongate and cylindrical, have a gnathocephalon that is broader apically, with serrated rugose pads dorsomedial of the anterior sensory lobes. The anterior sensory lobes are larger and more prominent and the serrated rugose pads laterad of the mouth lumen are larger and more numerous than in two *Campiglossa* spp. that have been described in similar detail. Behaviors of adults of *D. picciola* and *C. genalis* in southern California were similar, but differed in several respects from *D. picciola* on *C. officinalis* in India. Wing lofting by *D. picciola* and such unique aspects of its mating behavior in southern California as its copulatory induction behavior and mate guarding are described.

Key Words: Insecta, *Dioxyna picciola*, *D. sororcula*, nonfrugivorous Tephritidae, mating behavior, immature stages, Asteraceae, flower-head feeding

The genus *Dioxyna* is widespread in the New World, but is represented by only two species in North America, *D. picciola* (Bigot 1857) and *D. thomae* (Curran) (Foote et al. 1993). Of these two species, only the former occurs in California.

Dioxyna is closely related to *Campiglossa* (Merz and Freidberg 1994); Foote (1980) suggested that a thorough and detailed study of the New World species was required to further distinguish the species within these two genera. This paper provides the first de-

tailed description of the biology, immature stages, adult behavior, and host-plant relationships of *D. picciola* to compare with similar aspects of the life history and taxonomy of the immature stages of *Campiglossa genalis* (Thomson) (Goeden et al. 1994b). Behavioral comparisons of adults are made with reference to Headrick and Goeden (1995) between our findings in California and descriptions from India by Grewal and Kapoor for *D. sororcula* (1984).

MATERIALS AND METHODS

A planting of ornamental *Coreopsis* sp. in the garden of DHH at 340 m in Riverside, CA, provided the main site for observing the field behavior of *D. picciola* during 1991 and 1992. This and additional plantings of ornamental *Coreopsis* in the gardens of RDG and JAT at 260 to 370 m elevations in Riverside, California, were used to supplement 1-liter samples of mature flower heads collected by RDG and coworkers from wild hosts in southern California since 1980 (Goeden and Blanc 1986; Goeden 1985, 1987, 1989, 1992, 1994). Samples of mature and immature flower heads were returned to the laboratory for dissection, photography, description, and measurement, or for bulk cagings in glass-topped sleeve cages in the insectary of the University of California, Riverside at $27 \pm 1^\circ\text{C}$ and a 14-h photophase. A total of 1144 flower heads in six random subsamples of 200 heads each from 1-liter samples from wild hosts, plus 82 heads from cultivars, were dissected to study the immature stages of *D. picciola*. Four eggs, 20 larvae, and 4 puparia obtained from dissections were preserved in 70% EtOH for scanning electron microscopy (SEM). All other puparia were placed in separate glass rearing vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult emergence. Specimens for SEM later were hydrated to distilled water in a decreasing series of acidulated EtOH, critical-point dried, mounted on stubs, sputter coated with a gold-palla-

dium alloy, and studied with a JEOL JSM C-35 scanning electron microscope in the Department of Nematology, University of California, Riverside.

Most adults reared from isolated puparia were individually caged in 850-ml, clear-plastic, screen-topped cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cagings were used for longevity studies and oviposition tests. Virgin male and female flies obtained from emergence vials, as well as field-collected adults, were paired in clear-plastic petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey for direct observations, video-recording, and still-photography of their general behavior, courtship, and copulation (Headrick and Goeden 1995). Six pairs of flies were held together for at least 14 d and observations of their behaviors were made as opportunity allowed throughout each day. Field studies were conducted in the garden of DHH as noted above, in which adult reproductive behavior was described and quantified according to the methods developed and described by Headrick and Goeden (1995).

Plant names used in this paper follow Munz and Keck (1959) and Munz (1968, 1974); names for flower head parts follow Hickman (1993). Tephritid names and anatomical terms follow Foote et al. (1993), except for *picciola* (Norrbon, pers. comm. 1994); nomenclature used to describe the immature stages follows Goeden and Headrick (1990, 1991a, b, 1992), Headrick and Goeden (1990, 1991, 1993), and the telegraphic format of Goeden et al. (1993, 1994a, b). Means \pm SE are used throughout this paper. Voucher specimens of reared adults of *D. picciola* and its parasitoids reside in the research collections of RDG; preserved specimens of larvae and puparia are stored in separate collections of immature Tephritidae maintained by JAT and DHH.

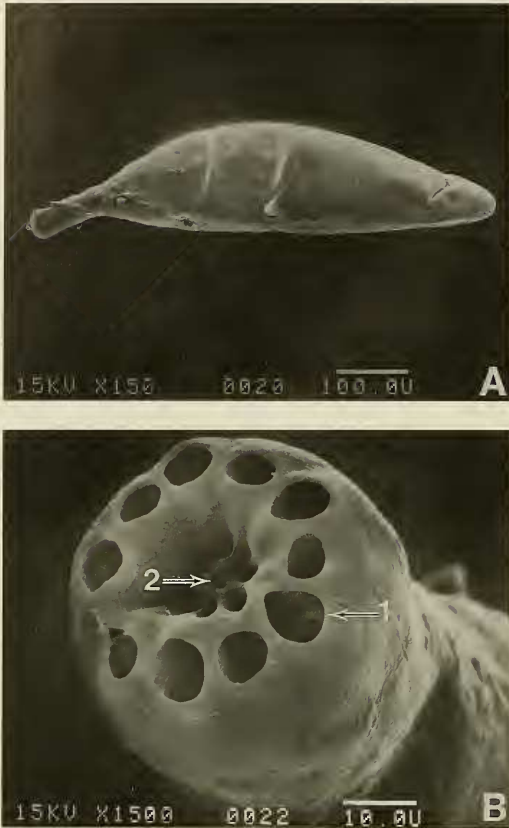


Fig. 1. Egg of *Dioxyna picciola*. (A) Habitus; (B) apical end of pedicel, 1—aeropyles, 2—micropyle.

RESULTS AND DISCUSSION

TAXONOMY

This species was generally known as *Dioxyna picciola* (Bigot) throughout North America (Novak 1974) and in California (Foote and Blanc 1963) until Hardy (1988) synonymized *D. picciola* with the cosmopolitan species, *D. sororcula*. Foote et al. (1993) adopted this change, as did we (Headrick and Goeden 1995) in deference to them, but A. L. Norrbom (pers. comm. 1994) has since indicated that the North American species is not *sororcula*. We ten-

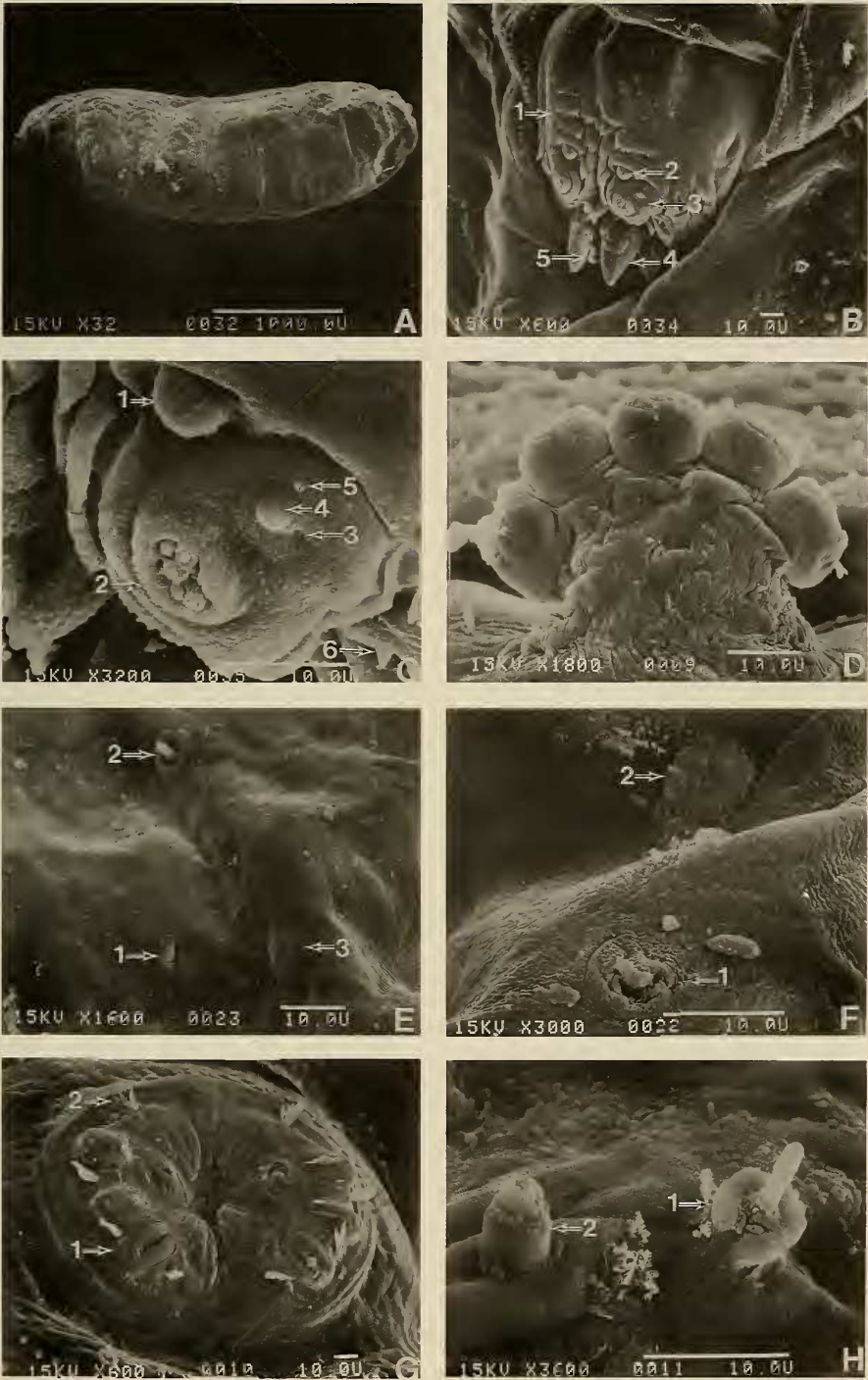
tatively use the name *D. picciola* in this paper. Munro (1957) discussed the genus *Dioxyna*, its relationship to *Campiglossa* (as *Paroxyna*, synonymized by Merz and Friedberg 1994) in the Afrotropical Region, and the separate taxonomic status of *D. picciola* and *D. sororcula*, but without resolving this question. Novak (1974) discussed and provided keys to the two U.S. species.

Benjamin (1934) sketched the egg and provided generalized descriptions and sketches of the third instar larva and puparium (as *Paroxyna picciola*). Phillips (1946) described the third instar and illustrated its cephalopharyngeal skeleton, anterior spiracles, and caudal end, including the posterior spiracles and interspiracular processes. Otherwise, the immature stages of *D. picciola* from North America are described and illustrated herein in detail for the first time.

Egg.—Body smooth, shiny white, elongate-ellipsoidal (Fig. 1A); six egg bodies averaged 0.78 ± 0.02 (range, 0.72–0.84) mm in length, 0.17 ± 0.01 (range, 0.16–0.18) mm in width; anterior end of the egg drawn out into a stout 0.14 ± 0.01 (range, 0.12–0.16) mm-long ($n = 4$), 0.08 mm-wide ($n = 2$) pedicel, apical end of pedicel slightly enlarged (Fig. 1A), aeropyles open apically on pedicel (Fig. 1B-1), a central, sunken, group of apertures may serve as the micropyle (Fig. 1B-2); posterior end of egg rounded, tapering gradually.

The egg sizes given herein are similar to those reported for *D. sororcula* in India by Jakhmola (1983); however, an elongate pedicel was not specifically mentioned. The egg morphology of two closely related species, *Campiglossa albiceps* (Loew) (Novak and Foote 1968) and *C. genalis* (Thomson) (Goeden et al. 1994b), differs considerably from *D. picciola*, as both species have a

Fig. 2. Third instar of *D. picciola*. (A) Habitus, anterior to left; (B) gnathocephalon, anterior view, 1—serrated rugose pads, 2—dorsal sensory organ, 3—anterior sensory lobe, 4—mouth hooks, 5—median oral lobe; (C) anterior



sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—stomal sense organ; (D) anterior thoracic spiracle; (E) lateral spiracular complex, metathorax, 1—spiracle, 2—stelex sensillum, 3—verruciform sensillum; (F) lateral spiracular complex, first abdominal segment, 1—spiracle, 2—verruciform sensillum; (G) caudal segment, posterior spiracular plates, 1—rima, 2—interspiracular process; (H) compound sensillum, 1—stelex sensillum, 2—medusoid sensillum.

non-elongated, mammiloid pedicel similar to most of the Tephritini that we have described thus far, *cf.*, Goeden et al. (1993, 1994b), Headrick and Goeden (1991), Goeden and Headrick (1991a). The aeropyle openings in these species circumscribe only the lateral aspect of the pedicel, not the apical end as in *D. picciola*.

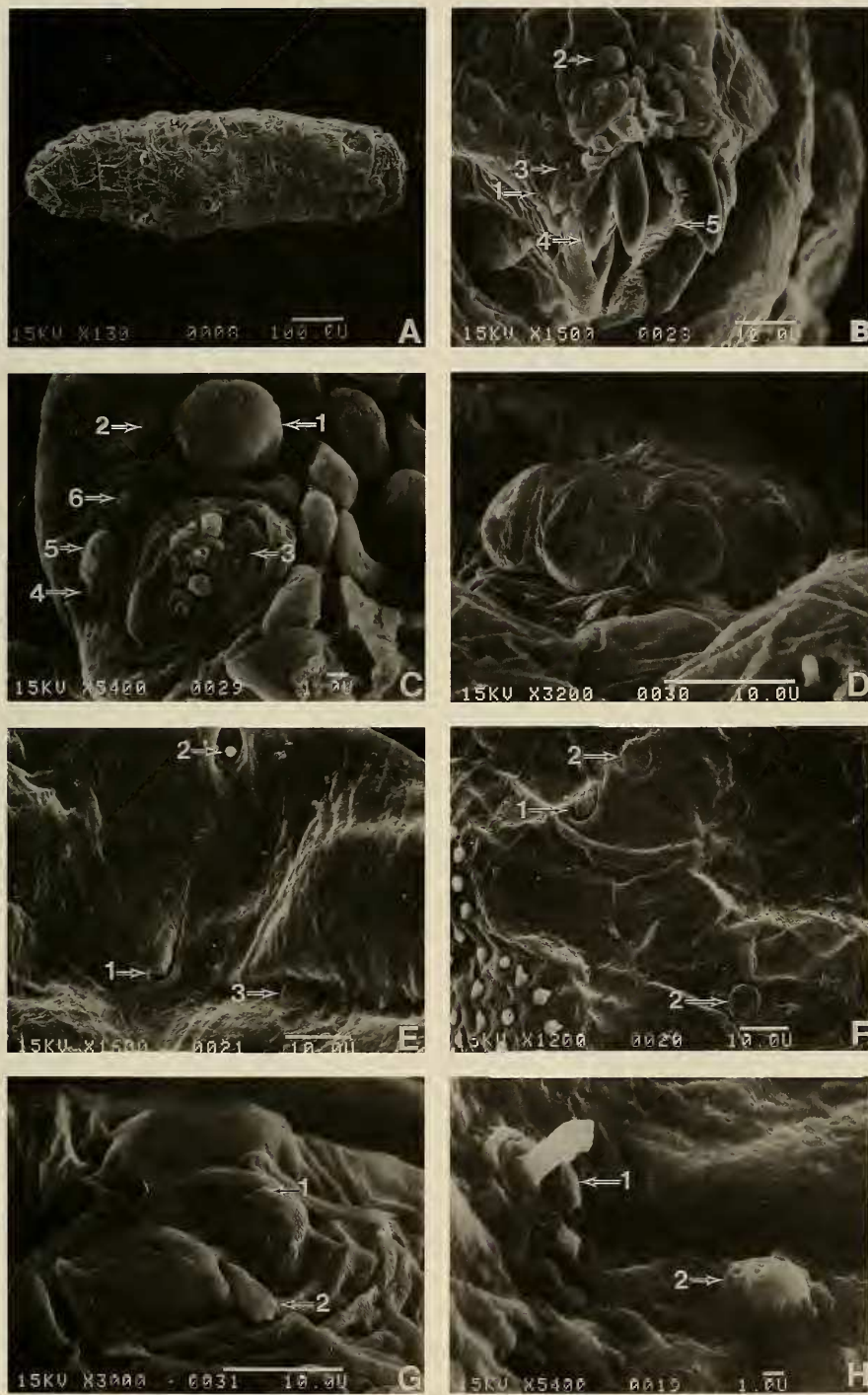
Third instar.—Elongate, cylindrical, anterior and posterior ends rounded, superficially smooth, minute acanthae circumscribe intersegmental areas (Fig. 2A); gnathocephalon conical with serrated rugose pads laterad and dorsomedial of anterior sensory lobes (Fig. 2B-1); dorsal sensory organ comprised of single, dome-shaped papilla dorsal to anterior sensory lobes (Figs. 2B-2, 2C-1); anterior sensory lobe (2B-3, 2C), bears terminal sensory organ (Fig. 2C-2), pit sensory organ (Fig. 2C-3), lateral sensory organ (Fig. 2C-4), and supralateral sensory organ (Fig. 2C-5); stomal sense organs ventrolaterad of anterior sensory lobes (Fig. 2C-6); mouth hooks bidentate, teeth stout, conical (Fig. 2B-4); median oral lobe laterally flattened, attached to labial lobe (Fig. 2B-5); anterior spiracles protruding, bearing five rounded papillae apically (Fig. 2D); metathoracic lateral spiracular complex consists of spiracle (Fig. 2E-1), stelex sensillum (Fig. 2E-2) and single verruciform sensillum (Fig. 2E-3); abdominal lateral spiracular complex consists of spiracle (Fig. 2F-1) and two verruciform sensilla (Fig. 2F-2); caudal segment bears posterior spiracular plates; posterior spiracular plates raised, bearing three oval rimae ca. 0.025 mm long (Fig. 2G-1), and four lanceolate interspiracular processes with two to four branches each, longest measuring 0.013 mm (Fig. 2G-2); stelex sensilla circumscribe margin of caudal segment; compound sensilla ventrad of posterior spiracular plates consist of stelex sen-

silla (Fig. 2H-1), and raised, medusoid sensilla with minute papillae (Fig. 2H-2).

The third instar of *Dioxyna picciola* closely resembles *C. albiceps* (Novak and Foote 1968) and *C. genalis* (Goeden et al. 1994b) morphologically, but is more elongate and cylindrical in body shape and the gnathocephalon is broader apically, with serrated rugose pads dorsomedial of the anterior sensory lobes. The anterior sensory lobes are larger and more prominent in *D. picciola* than in the two *Campiglossa* spp., and the serrated rugose pads laterad of the mouth lumen are larger and more numerous. The anterior thoracic spiracles are very similar in *D. picciola* and *C. genalis*, each bearing 4–5 rounded papillae; whereas, the anterior spiracles of *C. albiceps* bear 12–13 papillae (Novak and Foote 1968). The metathoracic lateral spiracular complex of *D. picciola* has only a single verruciform sensillum; whereas, *C. genalis* has two verruciform sensilla (Goeden et al. 1994b). The abdominal lateral spiracular complexes of *D. picciola* lack campaniform sensilla and the third verruciform sensilla reported for *C. genalis* (Goeden et al. 1994b). To date, *D. picciola* and *C. genalis* are the only species known with a stelex sensillum associated with the lateral spiracular complex, and the posterior spiracular plates and the type of sensory structures on them are similar. The compound sensilla of these two species also are similar to those of *Tephritis arizonaensis* Quisenberry (Goeden et al. 1993), *Trupanea bisetosa* (Coquillett), and *T. nigricornis* (Coquillett) (Knio et al. 1995).

Second instar.—Elongate cylindrical, anterior and posterior ends rounded (Fig. 3A); minute acanthae circumscribe intersegmental areas (Fig. 3A); gnathocephalon conical (Fig. 3B); rugose pads mediad and laterad of anterior sensory lobes, lateral pads ser-

Fig. 3. Second instar of *D. picciola*. (A) Habitus, anterior to left; (B) gnathocephalon, anterior view, 1—serrated rugose pads, 2—dorsal sensory organ, 3—stomal sense organ, 4—mouth hooks, 5—median oral lobe; (C)



anterior sensory lobe, 1—dorsal sensory organ, 2—sensillum, 3—terminal sensory organ, 4—pit sensory organ, 5—lateral sensory organ, 6—supralateral sensory organ; (D) anterior thoracic spiracle; (E) lateral spiracular complex, metathorax, 1—spiracle, 2—stelex sensillum, 3—verruciform sensillum; (F) lateral spiracular complex, first abdominal segment, 1—spiracle, 2—verruciform sensilla; (G) caudal segment, posterior spiracular plates, 1—rima, 2—interspiracular process; (H) compound sensillum, 1—stelex sensillum, 2—dome-shaped sensillum.

rated (Fig. 3B-1); dorsal sensory organ comprised of single, dome-shaped papilla dorsal to anterior sensory lobe (Fig. 3B-2, 3C-1); small sensillum laterad of dorsal sensory organ (Fig. 3C-2); anterior sensory lobes bear terminal sensory organ (Fig. 3C-3), pit sensory organ (Fig. 3C-4), lateral sensory organ (Fig. 3C-5) and supralateral sensory organ (Fig. 3C-6); stomal sense organs laterad of mouth lumen, serrated on ventral margins (Fig. 3B-3); mouth hooks bidentate (Fig. 3B-4); median oral lobe laterally flattened, ventrally attached to labial lobe (Fig. 3B-5); anterior spiracles dorso-lateral on posterior margin of prothorax, each bear five rounded papillae (Fig. 3D); metathoracic lateral spiracular complex consists of spiracle (Fig. 3E-1), stelex sensillum (Fig. 3E-2), and a verruciform sensillum (Fig. 3E-3); abdominal lateral spiracular complex consists of spiracle (Fig. 3F-1) and two verruciform sensilla (Fig. 3F-2); caudal segment bears the posterior spiracular plates; posterior spiracular plates bear three oval rimae ca. 0.013 mm long (Fig. 3G-1), and four, single remiform interspiracular processes, longest measuring 0.011 mm (Fig. 3G-2); stelex sensilla surround margin of caudal segment; compound sensilla ventrad of posterior spiracular plates consist of stelex sensillum (Fig. 3H-1), and dome-shaped sensillum (Fig. 3H-2).

The second instar differs from the third instar in being more cylindrical. The gnathocephalon of the second instar is conical, not as broad as that in the third instar. The serrated rugose pads located dorsomedial of the anterior sensory lobes on the third instar are lacking in the second instar. There also are fewer serrated rugose pads laterad of the mouth lumen in the second instar. A small sensillum located laterad of the dorsal sensory organ was found in the second instar, but not observed in the third instar. A similar sensillum was described from the first instar of *T. nigricornis* (Knio et al. 1995). Sensory structures are usually maintained in the third instar if they are present

in the earlier instars (Headrick and Goeden 1990). The lateral spiracular complexes on the thoracic and abdominal segments of the second instar are similar in placement and structure to those of the third instar. The posterior spiracular plates of the second instar are not as anatomically distinct as those of the third instar, the rimae are smaller and the interspiracular processes have not differentiated into multiple blades.

First instar.—Elongate cylindrical, anterior and posterior ends rounded (Fig. 4A); gnathocephalon smooth, lacking rugose pads (Fig. 4B); dorsal sensory organ is a single, dome-shaped papilla (Fig. 4B-1, 4C-1); anterior sensory lobes (Fig. 4B-2, 4C), bear the terminal sensory organ (Fig. 4C-2), pit sensory organ (Fig. 4C-3), lateral sensory organ (Fig. 4C-4), and supralateral sensory organ; stomal sense organs indistinct; mouth hooks bidentate, teeth conical (Fig. 4B-3); median oral lobe laterally flattened and ventrally attached to labial lobe (Fig. 4B-4); anterior spiracles not present; lateral spiracular complex not observed; posterior spiracular plates bear two oval rimae ca. 0.004 mm long (Fig. 4D-1), and four interspiracular processes, longest measuring 0.005 mm (Fig. 4D-2); compound sensilla not seen.

Puparium.—Light brown, elongate, cylindrical, smooth, rounded at both ends, acanthae circumscribe intersegmental areas (Fig. 5A); length 2.5 ± 0.03 (range, 2.37–2.88) mm, width 1.04 ± 0.01 (range, 0.86–1.18) mm ($n = 28$); anterior end bears the invagination scar (Fig. 5B-1) and raised anterior spiracles, each with 4–5 rounded papillae (Fig. 5B-2); posterior spiracular plates bear slightly raised oval rimae, ca. 0.034 mm long (Fig. 5C-1), and four interspiracular processes with 1–3 branches, longest branch measuring 0.014 mm (Fig. 5C-2).

DISTRIBUTION AND HOSTS

The North American distribution of *D. picciola* was mapped north of Mexico by Foote et al. (1993) to include most of the

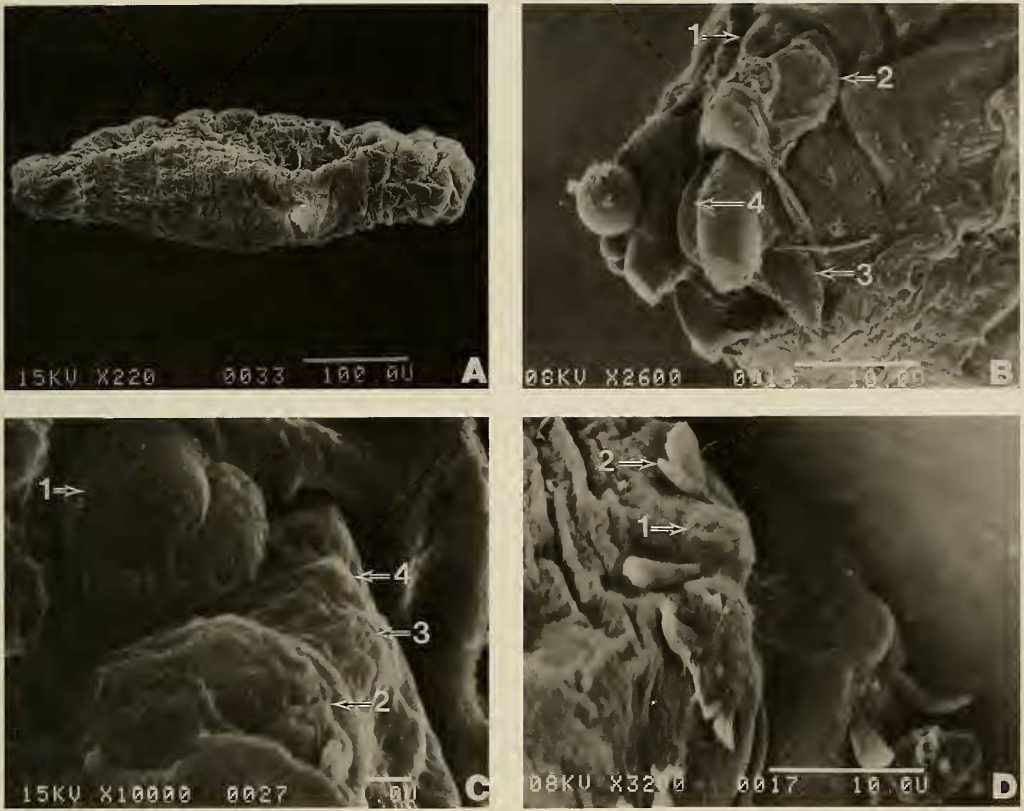


Fig. 4. First instar of *D. picciola*. (A) Habitus, anterior to left; (B) gnathocephalon, anterolateral view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—mouth hooks, 4—median oral lobe; (C) anterior sensory lobe, 1—dorsal sensory organ, 2—pit sensory organ, 3—lateral sensory organ, 4—rima; (D) caudal segment, posterior spiracular plates, 1—rima, 2—interspiracular process.

United States except for the New England States and the Province of Ontario, Canada, and eastward. Novak (1974) called its North American distribution “extensive”, and like Foote et al. (1993), noted the absence of collection records from “. . . the upper New England States, central plains, and portions of the northern Rocky Mountain area. Distribution northward is limited to the southern borders of Alberta, Saskatchewan, and Manitoba.” Records from central and southern California for *D. picciola* are common (Foote and Blanc 1963, Foote et al. 1993).

Wasbauer (1972) listed 10 species of *Bidens* and five species of *Coreopsis* as hosts of *D. picciola*. Goeden and Blanc (1986) added rearing records for an additional four

species of *Coreopsis*, so that there is little doubt that both genera are hosts of this tephritid, belonging as they do to the same subtribe Coreopsidinae of the tribe Heliantheae (Munz and Keck 1959). The record in Wasbauer (1972) for *Cosmos* sp., belonging to the same subtribe, accordingly also seems plausible, as do records for *Acanthospermum* and *Tagetes*, both in the tribe Heliantheae. However, additional disparate records for *D. picciola* in Wasbauer (1972) for *Aster* in the tribe Astereae and for *Helenium* in the tribe Helenieae accordingly are suspect. Since surveys were begun by RDG in southern California in 1980, *D. picciola* has only been reared from *Coreopsis* and *Bidens* spp. even though *Aster* and *Helenium* have been extensively sam-



Fig. 5. Puparium of *D. picciola*. (A) Habitus, anterior to left; (B) anterior end, 1—invagination scar, 2— anterior thoracic spiracle; (C) caudal segment, posterior spiracular plates, 1—rima, 2—interspiracular process.

pled as well (Goeden and Blanc 1986; Goeden, unpub. data). *D. sororcula* studied in India by Grewal and Kapoor (1984) occurred on *Calendula officinalis* L., a host belonging to still another tribe of Astera-

ceae, the Calenduleae (Munz and Keck 1959). Goeden (unpublished data) has not reared *D. picciola* from two, separate collections of naturalized *C. officinalis*, nor has this tephritid been reared or otherwise reported from this cultivar in California (Foote and Blanc 1963) or elsewhere in North America (Wasbauer 1972, Foote et al 1993). This, along with Munro's initial assessment (1957) and the behavioral data reported below, indicates that contrary to Hardy (1988), *D. picciola* and *D. sororcula* probably are distinct species; although, confounding this interpretation is the report by Grewal and Kapoor (1984) of the latter species attacking achenes of the introduced weed, *Bidens pilosa* L., in India.

BIOLOGY

Egg: Females lay eggs singly, alone or successively two-three times in a flower head. Eggs are inserted directly into soft achenes of ray florets in open flower heads, or laterally through the bracts from the outside of preblossom flower heads into the lobes of the ray florets (Fig. 6A, see Oviposition, below). The pedicels remain exposed, projecting from the achene (Fig. 6A), and oviposition scars on the phyllaries are surrounded by necrotic plant tissue (Fig. 6B).

Larva: The first instar emerges from a longitudinal slit in the basal posterior end of the egg and tunnels directly into a soft achene or lobe of a ray floret. The first instar tunnels horizontally through two-three young achenes while moving centripetally toward the center of the flower head. Multiple first instars infesting a single flower head apparently avoid contact, move independently within the flower head, and feed singly in different achenes as evidenced by their feeding tunnels (Fig 6C).

Second instars continue to feed singly inside the soft achenes (Fig 6D); they tunnel through five-six adjacent achenes moving horizontally above and parallel to the receptacle toward and into the central achenes. The damage incurred by this instar

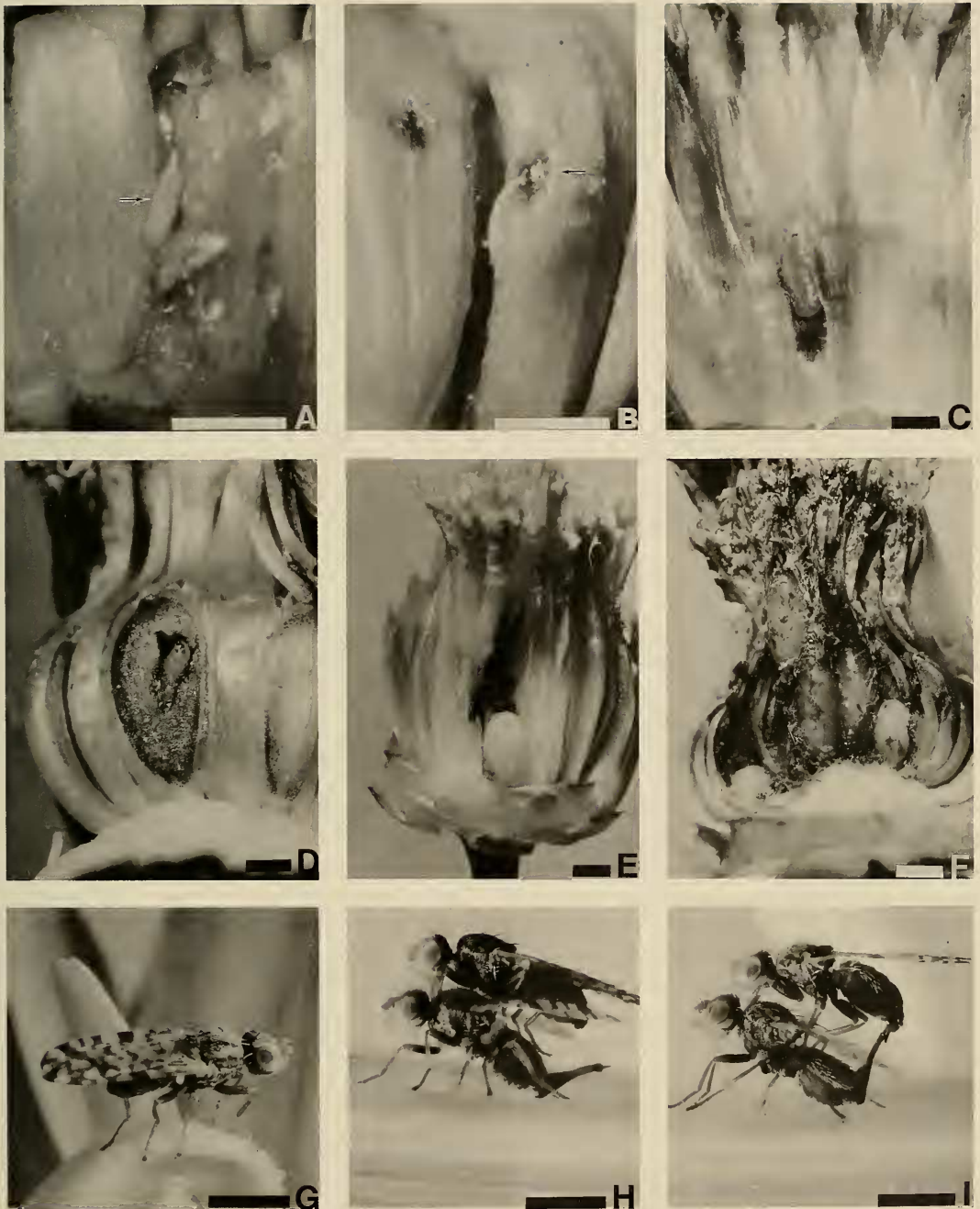


Fig. 6. Life stages of *D. picciola*. (A) Egg inserted into soft achenes of ornamental *Coreopsis* (arrow); (B) oviposition scars in phyllaries (arrow); (C) first instar mining soft achene in head of *C. bigelovii*; (D) second instar in soft achene of *Coreopsis* sp.; (E) full-size third instar feeding in center of flower head and scoring receptacle of *C. bigelovii*; (F) two central puparia and peripheral third instars in multiply-infested head of ornamental *Coreopsis* sp.; (G) newly emerged adult male; (H) pair of flies during copulatory induction behavior, (I) Same pair in copula. Bars = 1 mm.

Table 1. Ecological parameters (means) quantified for three host plants infested by third instars or puparia of *Dioxya picciola*.

	Host Plant Species		
	<i>C. bigelovii</i>	<i>C. sp. (small)</i>	<i>C. sp. (large)</i>
Average:			
No. of individuals			
per flower head	3.5	3.5	2.57
(Range)	(1-11)	(1-10)	(1-6)
Receptacle diameter	6.3	5.1	7.05
Puparia length	2.79	2.54	2.68
Puparia width	1.01	1.04	1.04
Achenes per flower			
head	68.0	51.3	85.4
Achenes damaged			
per flower head	28.2	18.67	11.8
Achenes damaged			
per individual	8.13	5.33	4.6
Percentage:			
Achenes damaged			
per individual	42%	36%	14%

persists and attacked achenes are aborted. Again, in flower heads containing more than one second instar, each larva occupies a separate achene (Fig. 6D). The receptacles of flower heads are not scored by larvae in this instar (Fig. 6D).

Third instars feed head-downward and separately, each within an individual central achene. All of the achene contents are consumed before the larva begins to score the receptacle. Mature third instars score a shallow, circular depression in the receptacle and remain head-downward feeding on the plant sap that accumulates in each depression (Fig. 6E). Feeding depressions were observed only in the centers of the receptacles where third instars congregated for feeding. Feeding depressions were approximately 0.6–0.7 mm in diameter.

Coreopsis bigelovii is a native desert annual with a receptacle that averaged 6.3 ± 0.2 (range, 5.1–7.9; $n = 15$) mm in diameter, each head of which contained an average of 68 ± 2.1 (range, 50–80) achenes (Table 1). An average of 3.5 ± 0.7 (range, 1–11) larvae and puparia of *D. picciola* were found in 15 infested flower heads (7.5%) of 200 heads dissected. These larvae

damaged 28.2 ± 4.7 (range, 12–60) achenes per head, or 8.1 achenes per larvae; 7 (49%) of these 15 infested heads had their receptacles scored, but only heads with >1 larvae. Twenty flower heads of the larger ornamental variety of *Coreopsis* averaged 7.1 ± 0.4 (range, 4.5–10.9) mm in receptacle diameter and each contained an average of 85.4 ± 9.6 (range, 50–185) achenes (Table 1). An average of 2.6 ± 0.3 (range, 1–6) larvae were found in 20 infested heads examined of this cultivar, 16 (73%) of which had their receptacles scored; these larvae damaged 11.8 ± 2.3 (range, 2–36) achenes per head or 4.6 achenes per larva. Eighteen (41%) of 44 smaller flower heads of the "Early Sunrise" variety of ornamental *Coreopsis* were infested; each head averaged 5.1 ± 0.2 (range, 4.0–8.0) mm in receptacle diameter and contained an average of 51.3 ± 3.4 (range, 35–75) achenes (Table 1). An average of 3.5 ± 0.6 (range, 1–10) individuals were found in infested flower heads, all of which had their receptacles scored. An average total of 18.7 ± 2.9 (range, 2–36) achenes were damaged in each head; an average of 8.1 achenes damaged per larva. The tephritid causes no eco-

onomic damage to ornamental *Coreopsis* in southern California because when oviposition occurs, the flower heads already are near or in full bloom and larval development occurs during flower head maturation, with most achenes left untouched, as documented above.

The receptacles of both ornamental varieties infested with single or multiple larvae were scored (Fig. 6E, F); therefore, the formation of feeding depressions was not density dependent as reported for *Paracantha gentilis* Hering in flower heads of native *Cirsium* thistles (Headrick and Goeden 1990). However, in the medium-sized flower heads of uncultivated *C. bigelovii*, only flower heads infested with two or more larvae showed feeding depressions. The centralized positions of the third instars, puparia, and feeding depressions of *D. picciola* (Fig. 6F) is found among some, but not all florivorous Tephritidae in southern California. This occurrence in the centers of flower heads was linked to resource sharing in the larger-size flowerheads of *Cirsium* thistles, within which Lepidoptera fed on the peripheral achenes (Headrick and Goeden 1990). Only larvae of *Trupanea jonesi* Curran occasionally shared the flower heads of *C. bigelovii* with *D. picciola* (Goeden 1985, 1992), except for one observation of a larva of an undetermined species of curculionid found feeding in the receptacle of a flower head that contained two third instars and a puparium of *D. picciola*.

Puparium.—Third instars began pupariation by turning 180° and facing away from the receptacle surface. Puparia were formed with their posterior ends resting in the shallow feeding depressions (Fig. 6F). In multiply-infested flower heads, the puparia were contiguous, clustered in the center of the flower head and covered by the dried remains of achenes, dried sap, pappus hairs, and frass (Fig. 6F). Third instars that did not score the receptacle also turned 180° from their feeding position head-downward in an individual achene and pupariated inside the hollowed out achene. In *C. bige-*

lovii, the achenes were much larger than the mature larva, and larvae that did not score the receptacle pupariated within the achene well above the level of the receptacle. In these instances, the basal fragment of the achene had acted as a conduit for the sap from the receptacle fed upon by the larva. In flower heads with multiple larvae, those that pupariated first were located centrally, followed later by the surrounding, peripheral larvae (Fig. 6F).

Adult.—Females emerge reproductively immature and showing few fat globules in their haemolymph. Their rudimentary ovarioles measured ca. 0.4 mm in length and females required ca. 3 weeks of feeding in the laboratory to mature eggs before mating and oviposition behaviors were expressed. Adults are long lived, with 12 females averaging 93.2 ± 7.22 (range, 49–203) d longevity in the laboratory, and 19 males (Fig. 6G) averaging 88.7 ± 4.5 (range, 62–129) d.

In laboratory mating trials adults were active from ca. 0900 to dusk. Both males and females rested, groomed, and fed within arenas and when observed in the field. Mating occurred throughout the day and into the night in laboratory arenas under artificial lighting, and with some pairs continuing in the dark under both the field and laboratory conditions.

Wing displays: Both sexes lofted their wings (*cf.* Goeden et al. 1994b, Headrick and Goeden 1995), but the wings were only raised slightly. Lofting in *D. picciola* involved extending both wings forward synchronously from the resting position in which both wings were held flat and slightly parted over the dorsum. Both wings were extended forward through ca. 20° and raised only slightly without any supination during extension. Both sexes also simultaneously raised their abdomens ca. 20° with each wing extension. The wing loft and abdominal flexure were concurrent and lasted ca. 1 sec. Lofting displays were observed while individuals were walking or while facing other individuals. Males also exhibited slight hamations over their abdomens

after such wing displays, similar to those reported for *Trupanea* spp. (Headrick and Goeden 1991, 1995). Thus, hamations followed lofting displays before the wings moved into a resting position. In the field, males exhibited wing displays during copulation and during encounters with other males; each of these displays is described below. Females were observed to exhibit slight asynchronous supinations when facing an intruder or other moving object as reported for many other tephritid species (Headrick and Goeden 1991, 1995). Females also displayed slight hamations after wing displays before returning their wings to a resting position.

Courtship: Twelve male-female encounters were observed in the laboratory in which males approached females in 7 of the 12 encounters. During all 12 approaches, both sexes displayed wing lofting coupled with abdominal raises, and on one occasion a male displayed abdominal pleural distension, but no other courtship or display behaviors were observed. Both sexes also visually oriented to the opposite sex as they passed each other in the arenas. Males oriented toward females, apparently visually, 8 times in one 2-h observation period and females oriented visually toward males twice in the same period. Females also raised their front legs toward advancing males, who then moved away ($n = 2$).

Courtship which led to mounting of the female by the male was observed twice in laboratory arenas, where the behaviors displayed by *D. picciola* were similar to those described for *Campiglossa genalis* (Goeden et al. 1994b). *Dioxyna picciola* males oriented toward females throughout the day in both field and laboratory observations; however, courtship was only observed in laboratory arenas (see Field Observations, below). During courtship males approached females head-on with their wings lofted, but raised higher than in the general lofting display described above. The wings were supinated ca. 45° and raised above the thorax ca. $70\text{--}80^\circ$ from the horizontal. In one of

the two courtship observations, the male approached a female and held his wings lofted and still. The female also stood still. He then expanded his abdominal pleura, extended his mouthparts, wagged them back and forth and raised his front legs over his head. The female did not move as the male next walked onto her dorsum, turned 180° , grasped her with his legs, and began copulatory induction behavior. In the other observation, the male lofted his wings, distended his abdominal pleura, wagged his extended mouthparts, then quickly climbed on top of the female without raising his front legs. A total of six mountings was observed; two followed courtship and four were opportunistic in which males mounted females contacted by chance movements within the arena and without prior displays. In the remaining male-female encounters, ($n = 8$), females decamped ($n = 4$), remained still ($n = 1$), or moved away, then returned to a male ($n = 3$).

Mounted males turned 180° and grasped the female with their front legs on the humerus of her thorax; the foretarsi rested behind the female's head. The middle legs grasped the thorax behind the wing bases and the hind legs rested on top of the abdomen. Copulatory induction behavior began from this position. In all mountings, copulatory induction behavior was initiated and copulation followed ($n = 6$), i.e. no female was observed to successfully reject a male once he mounted her.

Copulatory Induction Behavior (CIB): Mounted males began CIB by pulling upward on a female's abdomen with the hind legs. A mounted female raised her front legs above her head in an attempt to grasp the male. This was observed when a male's front tarsi touched the female's head, but did not occur when his tarsi remained on the female's thorax. All females groomed their abdomens vigorously with their hind legs just after being mounted. Mounted females spread their wings ca. 80° from the midlines of their bodies. Wing spreading was also observed after disengagement (see

below). The wings of males remained slightly overlapped during copulation. Females continued to resist mounted males and resisted having their abdomens pulled upwards. Mounted males displayed CIB different from other species of non-frugivorous tephritids examined thus far (Headrick and Goeden 1995). The hind tarsi of a mounted male were flattened against the dorsum of a female's abdomen, in a line parallel with the long axis of her body. Males rubbed their hind tarsi asynchronously against the first three abdominal tergites of the females, posteriorly to anteriorly, in rapid bursts that lasted 1–5 sec interspersed with pauses of 1–30 sec. CIB continued until a female raised her ovipositor and partly exerted the aculeus; no female was observed to be unresponsive to CIB ($n = 17$). Females responded by raising the ovipositor upward ca. 45° with respect to the abdomen (Fig. 6H). After the ovipositor was raised, the aculeus was exerted slightly, exposing its tip. Females continued to raise the abdomen and ovipositor unassisted until the ovipositor was perpendicular to the abdomen of the male (Fig. 6I). The male then released the female's abdomen and began vigorous CIB with the hind legs to further induce the female to hold her abdomen upward in the extended position. When females raised the ovipositor fully, males moved posteriad, extending their abdomens to engage the partially exerted tip of the aculeus with the surstylii (Headrick and Goeden 1995). This engagement was only successful on the first attempt in one of 17 observations. More often, the males missed engaging the aculeus and females lowered the abdomen and ovipositor to a resting position. This stimulated a male to continue with vigorous CIB and the female responded by again raising the ovipositor, partly exerting her aculeus, and then lifting her abdomen. The male then again extended his abdomen in an attempt to engage the raised ovipositor apex with his surstylii on the aculeus. If he was suc-

cessful, he moved forward again and intromission began.

Copulation: Fourteen pairs were observed *in copula*, six of which were observed for the total length of their mating sequence. These 6 pairs repeated copulations an average of 3 times (range, 2–6) with the male remaining mounted on the female. Five pairs remained together an average of 6.2 (range, 4–8) h. One of the pairs remained together for total of 28 h! Single copulation events averaged 1.0 (range, 0.5–1.25; $n = 19$) h.

Copulation began with males successfully engaging the margins of the aculeus with the prenisetae of the surstyli (Headrick and Goeden 1995). Once engaged, females fully exerted the aculeus, thus raising the male's abdomen and exposing the cloaca of the aculeus. The aculeus was perpendicular to the long axis of the male's abdomen, as is typical of some *Campiglossa* spp. (Goeden et al. 1994b, Headrick and Goeden 1995). The aedeagus uncoiled and entered the ventral flap from behind and above. When the ventral flap opened, the distiphallus could be seen entering and moving down the aculeus, which caused the latter to expand. The eversible membrane also expanded as the distiphallus passed through it; therefore, the progress of aedeagal insertion could be monitored. The distiphallus entered the ventral flap and reached the oviscape in less than 1 sec ($n = 2$). Males pushed against the aculeus as the aedeagus was further inserted, while females simultaneously applied pressure on the aculeus against the male, which caused expansion of the eversible membrane. After ca. 2 min, males had fully inserted the aedeagus, and the epandrium rested against the margin of the partially exerted eversible membrane ($n = 2$). During copulation, females became agitated and males responded with CIB until they again were quiet. Males also displayed synchronous wing lofting when approached by other males while in copula, both in the field and laboratory arenas. The wings were held at ca. 45° away from the midline of the

body, slightly raised and supinated to ca. 45° with respect to the substrate.

Six disengagements were observed, three in the field and three in laboratory arenas. Females typically became agitated before disengagement, which began with partial extension of the aculeus. Males responded by raising their body and pushing downward on the dorsum of the female's abdomen with the hind legs. Males continued rubbing and pushing down on the female's abdomen, and females further exerted the aculeus. The aedeagus was withdrawn by actions of both the male and female. Males pulled the aedeagus free by raising the abdomen, while females lowered their abdomens, but kept the ovipositor flexed upward and the aculeus extended. Once free, males recoiled the aedeagus either with or without the use of the hind legs and females lowered their ovipositors. Grooming commenced immediately after disengagement. Males rested their hind legs on top of the female's abdomen, but continued to grasp the female with the front and middle legs.

Males initiated CIB after disengaging and pairs re-mated with the males never having moved off of the female. *Campiglossa genalis* also exhibited this type of mate-guarding behavior (Goeden et al. 1994b). In the field, *D. picciola* pairs disengaged and males remained on females while they oviposited into flower heads, after which CIB was initiated and copulation occurred at least once again ($n = 6$). In laboratory arenas, males remained on females and soon initiated CIB without the females having oviposited. Both *D. picciola* and *C. genalis* display prolonged contact in which males remain on the dorsa of females after removal of the aedeagus (Goeden et al. 1994b, Headrick and Goeden 1995). CIB is typically initiated again and copulation follows. Copulations are repeated from 2-7 times in individual mating episodes.

Waste elimination: Waste elimination by males was typical for other tephritids examined thus far (Headrick and Goeden 1995). However, females exerted the acu-

leus, placing the tip onto the substrate, formed a subapical waste droplet from the cloaca onto the substrate, then retracted the aculeus without dragging it and thus left behind a small droplet.

Defense: Females raised the front legs toward approaching individuals in a defensive posture ($n = 2$) and both sexes displayed asynchronous wing supination extensions toward moving objects. Males did not raise the front legs in defense.

Territoriality: Males displayed aggression toward each other in the field, but no specific territorial displays or behaviors were observed.

Field observations: Distribution and abundance. Only one to five adults were observed at any one time on or near their individual host plants. Mating pairs were first observed after at least some of the flower heads had opened. Prior to flowering, individuals were observed resting singly, head-down on peduncles or leaves, or exploring the immature flower heads. Females did not probe the immature heads with their ovipositors. Pairs in copula were observed on peduncles, leaves and flower heads in all stages. Mated females moved from one head to another by flying short distances with males still mounted on their dorsa, but females did not move among flower heads while in copula. Adults remained on their host plant for feeding, resting, grooming, copulation and oviposition. Adults remained on the upper portions of plants until after dusk, but then were not observed on plants until the next morning. Presumably, they moved down into the centers of crowns during the night. Adults of *D. picciola* were never abundant; a maximum of five was observed on any one plant.

Male-female interactions: Individual males rested on peduncles, leaves and flower heads visually scanning the plant. Females were observed commonly on the tops or the undersides of flower heads, as well as on leaves and peduncles. Males encountered females only on flower heads ($n = 6$).

Courtship was not observed and females usually took flight when approached by males.

Three mated pairs were observed during field observations. The three pairs rested on different parts of the plant while in copula, but most commonly on flower heads. Females walked on flower heads continuously while in copula. Males in copula displayed their wings when approached by other individuals or when the females became agitated. Males spread their wings to ca. 45° from the midline of the body and vibrated them forward for ca. 1 sec, keeping them horizontal to the substrate, then returned them to their resting position. Wing displays were continued until the female became quiet or the other intruding individual moved away.

Oviposition.—When a pair disengaged, the male remained on top of the female and she began to explore the centers of blossoms for oviposition. Females also spread their wings to ca. 90° from the midline of the body without supination after disengagement, while searching and probing for oviposition sites. During oviposition, ($n = 8$), a female bent her abdomen downward, exerted her aculeus in between the outer florets and ray flowers and deposited her eggs singly. Males, with difficulty, remained mounted on females during oviposition. Males groomed while females probed and oviposited. Females groomed after oviposition. Males resumed CIB after females probed flower heads ($n = 2$), or after one to three eggs were laid ($n = 3$), or after the female moved to a new flower head ($n = 1$), usually within ca. ½ h of disengagement. One pair stayed together for 28 h, during which time they copulated and oviposited three times in one day, remained *in copula* on one flower head overnight, and copulated and oviposited again three times during the following day.

Grewal and Kapoor (1984) described the courtship and mating behaviors of *D. sororcula* on *Callendula officinalis* in India in the field and laboratory. They described the

floral discs of flower heads of *C. officinalis* as “sites of assembly” on which 93% of male-female encounters took place. Copulations were attempted in 53% of all encounters and 91% were successful. They also described aggressive behavior between adults involving synchronous wing supinations, front leg elevations, and charging behaviors similar to those limitedly observed in the present study. However, certain differences in the courtship and copulation behaviors of these geographically disparate populations were evident. For example, Grewal and Kapoor (1984) did not report male courtship displays, only that males rapidly mounted ovipositing females. Grewal and Kapoor (1984) also reported that mounted males did not show any wing displays when approached by other males; however males in both the field and laboratory settings displayed their wings at intruders. In the present study, courtship displays were observed in the laboratory, and unlike *D. sororcula* in India, males did not mount females while they were ovipositing. Grewal and Kapoor (1984) reported that males copulated with females an average of four times during a single mating episode and that between copulations females laid 2–5 eggs singly. We similarly observed three copulations per mating episode and 1–3 eggs laid between copulations, but again, no males mounting ovipositing females. Grewal and Kapoor (1984) also reported that pheromones were not involved in courtship or copulation and that conspecific recognition was by vision only. In the present study, abdominal pleural distension was observed, and thus, pheromone mediated behavior cannot be entirely dismissed (Headrick and Goeden 1995). Grewal and Kapoor (1984) also did not report the CIB described above, which uniquely involved mounted males: rubbing the tops of female’s abdomens with their hind tarsi; instead, they reported CIB involving male mouthpart pumping and repeated touching inner vertical and postvertical bristles of the female, to which she responded by pumping

her mouthparts for 10–30 seconds, then jerked her head upward while elevating her ovipositor. They also observed that the mounted male cleaned his legs and head, and the female while mounted cleaned her wings, head, and legs before initiating CIB and achieving intromission.

Seasonal history.—*Dioxya picciola* can be designated a “late aggregated attacker” among the trophic strategies proposed by Zwölfer (1988). In southern California, wild *Coreopsis* spp. begin flowering in the spring (April–May) and this continues through the summer months (June–August) on cultivated varieties. F₂ adults produced on *Coreopsis* and F₃ adults produced on *Bidens* and overwintered from the previous year, aggregate on newly-flowering *Coreopsis* for mating and oviposition in the late spring and early summer (April–June). Development of the larval stages is completed in ca. 3 weeks, pupariation occurs, and adults emerge ca. 2 weeks later. Some of these adults continue reproduction on their host plants if they are still in bloom, e.g. ornamental *Coreopsis*, and produce a second generation in the late summer (July–August). The F₂ adults emerge by the fall (September) to disperse to other locales where alternate host plant species such as *Bidens* spp. are in bloom to reproduce an F₃ generation, or to overwinter until the following season.

Natural enemies.—The following chalcidoid Hymenoptera were reared from puparia as primary, solitary, larval-pupal endoparasitoids: *Eurytoma* sp. (Eurytomidae) and *Halticoptera* sp. (Pteromalidae).

ACKNOWLEDGMENTS

Once again, we sincerely thank A. C. Sanders, Curator of the Herbarium, Department of Botany and Plant Sciences, University of California, Riverside, for identification of plants. Serguei Triapitsyn, Principal Museum Scientist, Department of Entomology, University of California, Riverside, identified or facilitated identification of the parasitoids by H. E. Anderson,

Huntington Beach, CA. Our thanks also to F. L. Blanc, A. L. Norrbom, J. A. Novak, and G. J. Steck for their helpful reviews of drafts of the manuscript.

LITERATURE CITED

- Benjamin, F. H. 1934. Descriptions of some native trypetid flies with notes on their habits. U.S. Department of Agriculture Technical Bulletin 401. 95 pp.
- Bigot, J. M. F. 1857. Dipteros, pp. 328–349. In R. de la Sagra, Historia fisica politica y natural de las Isla de Cuba, Segunda parte. Historia natural. Paris (1856). 371 pp.
- Foote, R. H. 1980. Fruit fly genera south of the United States. U.S. Department of Agriculture Technical Bulletin 1600. 77 pp.
- Foote, R. H. and F. L. Blanc. 1963. The fruit flies or Tephritidae of California. Bulletin of the California Insect Survey 7: 1–117.
- Foote, R. H., F. L. Blanc, and A. L. Norrbom. 1993. Handbook of the Fruit Flies (Diptera: Tephritidae) of America North of Mexico. Cornell University Press, Ithaca.
- Goeden, R. D. 1985. Host-plant relations of native *Trupanea* spp. (Diptera: Tephritidae) in southern California. Proceedings of the Entomological Society of Washington 87: 564–571.
- . 1987. Host-plant relations of native *Urophora* spp. (Diptera: Tephritidae) in southern California. Proceedings of the Entomological Society of Washington 89: 269–274.
- . 1989. Host plants of *Neaspilota* in California (Diptera: Tephritidae). Proceedings of the Entomological Society of Washington 91: 164–168.
- . 1992. Analysis of known and new host records for *Trupanea* from California (Diptera: Tephritidae). Proceedings of the Entomological Society of Washington 94: 107–118.
- . 1994. Analysis of known and new host records for *Paroxyna* from California (Diptera: Tephritidae). Proceedings of the Entomological Society of Washington 96: 281–287.
- Goeden, R. D. and F. L. Blanc. 1986. New synonymy, host, and California records in the genera *Dioxya* and *Paroxyna* (Diptera: Tephritidae). Pan-Pacific Entomologist 62: 88–90.
- Goeden, R. D. and D. H. Headrick. 1990. Notes on the biology and immature stages of *Stenopa affinis* Quisenberry (Diptera: Tephritidae). Proceedings of the Entomological Society of Washington 92: 641–648.
- . 1991a. Life history and descriptions of immature stages of *Tephritis baccharis* (Coquillett) on *Baccharis salicifolia* (Ruiz and Pavon) Persoon in southern California (Diptera: Tephritidae). Pan-Pacific Entomologist 67: 86–98.

- . 1991b. Notes on the biology, hosts, and immature stages of *Tomoplagia cressoni* Aczél in southern California (Diptera: Tephritidae). Proceedings of the Entomological Society of Washington 93: 549–558.
- . 1992. Life history and descriptions of immature stages of *Neaspilota viridescens* Quisenberry (Diptera: Tephritidae) on native Asteraceae in southern California. Proceedings of the Entomological Society of Washington 94: 59–77.
- Goeden, R. D., D. H. Headrick, and J. A. Teerink. 1993. Life history and descriptions of immature stages of *Tephritis arizonaensis* Quisenberry (Diptera: Tephritidae) on *Baccharis sarothroides* Gray in southern California. Proceedings of the Entomological Society of Washington 95: 210–222.
- . 1994a. Life history and description of immature stages of *Procecidochares flavipes* Aldrich (Diptera: Tephritidae) on *Brickellia* spp. in southern California. Proceedings of the Entomological Society of Washington 96: 288–300.
- . 1994b. Life history and description of immature stages of *Paroxyna genalis* (Thomson) (Diptera: Tephritidae) on native Asteraceae in southern California. Proceedings of the Entomological Society of Washington 96: 612–629.
- Grewal, J. S. and V. C. Kapoor. 1984. Courtship and mating behaviour in the fruit fly, *Dioxyna sororcula* (Wied.) (Diptera: Tephritidae). Australian Journal of Zoology 32: 671–676.
- Hardy, D. E. 1988. Fruit flies of the subtribe Gastrozonia of Indonesia, New Guinea and the Bismarck and Solomon Islands (Diptera, Tephritidae, Trypetinae, Acanthonevrini). Zoologica Scripta 17: 77–121.
- Headrick, D. H. and R. D. Goeden. 1990. Description of the immature stages of *Paracantha gentilis* (Diptera: Tephritidae). Annals of the Entomological Society of America 83: 220–229.
- . 1991. Life history of *Trupanea californica* Malloch (Diptera: Tephritidae) on *Gnaphalium* spp. (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 93: 559–570.
- . 1993. Life history and description of immature stages of *Aciurina thoracica* (Diptera: Tephritidae) on *Baccharis sarothroides* in southern California. Annals of the Entomological Society of America 86(1): 68–79.
- . 1995. Reproductive behavior of California fruit flies and the classification and evolution of Tephritidae (Diptera) mating systems. Studia Dipterologica 1(2): 194–252.
- Hickman, J. C. (ed.). 1993. The Jepson Manual. University of California Press, Berkeley and Los Angeles.
- Jakhmola, S. S. 1983. Niger grain fly, *Diozina sororcula* (Wiedemann), a serious pest of niger in central India. Journal of the Bombay Natural History Society 80: 439–440.
- Knio, K. M., R. D. Goeden, and D. H. Headrick. 1995. Comparative descriptions of the immature stages and biologies of *Trupanea nigricornis* (Coquillett) and *T. bisetosa* (Coquillett) (Diptera: Tephritidae). Annals of the Entomological Society of America 88: (in press).
- Merz, B. and A. Freidberg. 1994. Nomenclatural changes in the Tephritidae (Diptera). Israel Journal of Entomology 28: 171–172.
- Munro, H. K. 1957. Trypetinae. In Ruwenzori Expedition, 1934–1935. British Museum (Natural History) 2(9): 853–1054.
- Munz, C. A. 1968. Supplement to A California Flora. University of California Press, Berkeley.
- . 1974. A Flora of Southern California. University of California Press, Berkeley.
- Munz, C. A. and D. D. Keck. 1959. A California Flora. University of California Press, Berkeley.
- Novak, J. A. 1974. A taxonomic revision of *Dioxyna* and *Paroxyna* for America north of Mexico. Melanderia 16: 1–53.
- Novak, J. A. and B. A. Foote. 1968. Biology and immature stages of fruit flies: *Paroxyna albiceps* (Diptera: Tephritidae). Journal of the Kansas Entomological Society 41: 108–119.
- Phillips, V. T. 1946. The biology and identification of trypetid larvae. Memoirs of the American Entomological Society 12, 161 pp.
- Wasbauer, M. W. 1972. An annotated host catalog of the fruit flies of America north of Mexico (Diptera: Tephritidae). California Department of Agriculture, Bureau of Entomology Occasional Papers No. 19, 172 pp.
- Wiedemann, C. R. W. 1830. Ausser europäische zweiflügelige insekten, vol. 2.
- Zwölfer, H. 1988. Evolutionary and ecological relationships of the insect fauna of thistles. Annual Review of Entomology 33: 103–122.